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Predator Deterrence by Flexible Shell Extensions of the Horse Mussel *Modiolus modiolus*

by

MARY M. WRIGHT AND LISBETH FRANCIS

Biology Department, Bates College,
Lewiston, Maine 04240

Abstract. Flexible, tapering hairs, or awns, on the periostracum of the horse mussel *Modiolus modiolus* discourage attachment by the predatory whelk *Thais lapillus.* This conclusion is based on laboratory preference tests demonstrating a higher frequency of attachment to the hairless blue mussel *Mytilus edulis.* Removal of the awns of the horse mussel results in more nearly equal attachment to both mussel species. To our knowledge, this is the first time that a selective advantage has been demonstrated experimentally for any periostracum.

INTRODUCTION

Two mussel species occur commonly along the rocky coast of Maine. The blue mussel *Mytilus edulis* (Linnaeus, 1758) is found in bays and estuaries and on exposed promontories at various levels in the mid to low intertidal (Seed & Brown, 1975; Menge, 1976). In contrast, the horse mussel *Modiolus modiolus* (Linnaeus, 1758) extends from the low intertidal to subtidal regions (Brown & Seed, 1977).

The most obvious morphological difference between the shells of these two mussels is the awns (hairy projections of the periostracum at the exposed posterior margin), which are present on *Modiolus modiolus* but are absent from *Mytilus edulis.*

The dog whelk *Thais lapillus* (Linnaeus, 1758) is a major intertidal predator that commonly attacks the blue mussel (Menge, 1976), and at least occasionally attacks the horse mussel (personal observation, MMW). *Thais* attacks bivalves mechanically by drilling with the radula, and chemically by dissolving the shell with secretions from the accessory boring organ (Gabriel, 1981).

Seed & Brown (1975) report that during their laboratory experiments, *Thais lapillus* never attacked the horse mussel; Nielsen (1975) suggests that the hairy or spiny shell texture may discourage attack by *Buccinum undatum* Linnaeus, 1758, a whelk that attacks bivalves by wedging the lip of its own shell between the open valves to hold them apart, then reaching in to tear off bits of flesh.

We suspect that the hairy periostracum of *Modiolus modiolus* might discourage attachment and boring by *Thais lapillus,* which depends on prolonged, close contact with prospective prey in order to attack and consume it.

Previous to this study, the only characteristic of bivalve shells actually shown to hamper predation by drilling gastropods was a greatly thickened valve (Vermeij, 1978).

MATERIALS AND METHODS

Collection and Holding of Animals

Animals were collected occasionally from 16 October 1982 to 9 March 1983 on Bailey Island, Maine, a few hundred meters from a section of rocky exposed coastline called "The Giant Staircase." Freshly caught whelks were isolated from prey and allowed to adapt to aquarium conditions for at least 4 days.

All animals were kept in a filtered recirculating seawater system in which one third of the water was replaced each week by ocean water that had been collected and allowed to stand for at least a week. Temperature, salinity, and pH were maintained within natural limits (8.5 to 11°C; 28 to 32 ppt.; and 7.4 to 7.5 respectively). The tanks received light from several large windows nearby and from fluorescent ceiling lights.

Design of Predator Choice Experiments

Three mussels of each species were selected, approximately matched for size (4 to 8 cm long), and arranged alternately on a sheet of plastic at one end of a five gallon aquarium. In each trial a different set of 20 whelks was placed in rows with their anterior ends directed toward

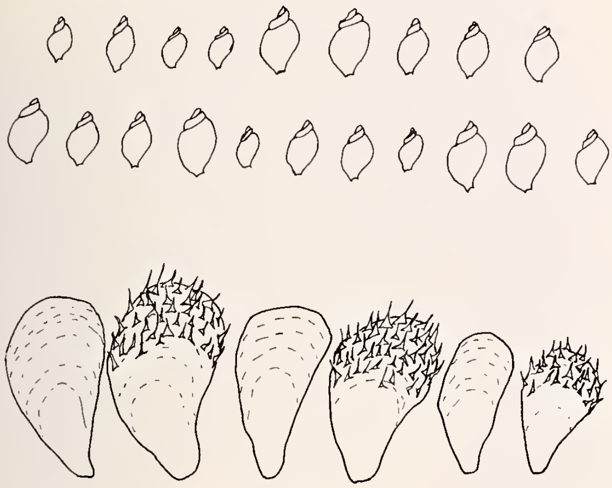

Figure 1

Spacing and arrangement of mussels (*Modiolus modiolus* with the awned periostracum, and *Mytilus edulis* with the smooth periostracum) and whelks (*Thais lapillus*) at the outset of laboratory predator choice trials.

the posterior margins of the mussels (Figure 1). This seemed a suitable testing arrangement, because in the field the mussels usually are wedged into crevices or between neighboring mussels with only the posterior margins exposed. After 24 h the number of whelks actually attached to each species of mussel was recorded. To minimize the possibility that the whelks were following old whelk mucus trails from previous trials, a new sheet of plastic was secured to the bottom of the tank and the mussels were scrubbed with a wet brush before each trial.

In a second set of experiments, the shells of all mussels were scraped with a razor blade before they were placed in tanks. This treatment effectively removed the awns of *Modiolus modiolus.*

RESULTS

With the periostracum of the mussels intact, 142 of the whelks attached to the smoother valves of *Mytilus edulis,* while only 23 attached to the hairy valves of *Modiolus modiolus* (31 trials involving 620 whelks). In these trials, the whelks attached to *Mytilus edulis* much more frequently than predicted by chance (Chi-square test for goodness of fit, $\chi^2 = 86$, $P \ll 0.001$). When all of the mussels were scraped, which effectively removed the awns from the horse mussel, a total of 99 whelks attached to *Mytilus edulis,* while 72 attached to the awnless specimens of *Modiolus modiolus* (28 trials involving 560 whelks). While the whelks continued to show a slight preference for *Mytilus edulis* when the awns of *Modiolus modiolus* were removed ($\chi^2 = 8.5$, $P < 0.005$), this preference was much less marked than when the periostracum was intact (2 × 2 test of independence, $\chi^2 = 73$, $P \ll 0.001$).

DISCUSSION

Along the rocky intertidal of New England, natural or artificial exclusion of the predatory whelk *Thais lapillus* results in monopolization of the primary space by *Mytilus edulis,* while in areas of heavy whelk predation, the blue mussel is commonly eliminated (MENGE & SUTHERLAND, 1976). Intense predation by invertebrates of the lower shore and subtidal apparently prevents the establishment of subtidal populations of *Mytilus edulis* (SEED, 1969).

Predation levels are higher and survival rates lower for small specimens of *Modiolus modiolus* than for larger ones, and rapid growth of smaller individuals results in escape in size from predation (SEED & BROWN, 1975). This kind of selective pressure should favor the evolution of mechanisms that discourage predation, especially on smaller individuals.

Our experiments show that the shell awns of *Modiolus modiolus* are an effective predator deterrent discouraging attachment by the whelk *Thais lapillus.* The fact that smaller horse mussels have more awns may be another indication of the importance of predation and predator deterrence among small, vulnerable individuals. The presence of these protective shell awns may allow *Modiolus modiolus* to live below *Mytilus edulis* in the lower intertidal and subtidal, where predator pressure is relatively intense. Further work is presently under way to determine whether the awns also discourage attack by other common predators such as the starfish *Asterias vulgaris* (MENGE, 1979).

It is possible that shell awns and various other kinds of shell sculpturing are advantageous not only because they make attachment more difficult, but also because they make an undesirable prey species easy for a prospective predator to recognize and reject. Using crabs as predators and mussels as prey, ELNER & HUGHES (1978) demonstrated the importance of recognition time in determining the selectivity of a predator. Foraging theory predicts that a predator that cannot distinguish quickly between a preferred prey item and a common, less desirable one, will take relatively large numbers of the less preferred type. Anything that makes a less preferred prey species easy to recognize could have a large selective advantage in such a situation. In addition to making *Modiolus modiolus* more difficult to approach and attack, the awns on the shell may make this species easier to recognize and reject by predators searching for more desirable prey.

While there has been considerable work on the structure and formation of the periostracum (reviewed by SALEUDDIN & PETIT, 1983; WAITE, 1983), there has been little experimental work on periostracum function (reviewed by CLARK, 1976). In general, the periostracum is presumed to protect the calcareous layers of the shell from erosion (FRETTER & GRAHAM, 1962; SOLEM, 1974) and to play an important role in mineralization of the shell (CLARK, 1976).

This is the first demonstration that the periostracum of a bivalve can discourage predation by a drilling gastropod.

To our knowledge, it is also the first time that a specific selective advantage has been demonstrated experimentally for any periostracum.

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